Ontogeny of Positional Behavior in Captive Silvered Langurs (*Trachypithecus cristatus*)

A Senior Honors Thesis

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by

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ABSTRACT

Compared to most other mammalian groups, primates are known for the great diversity of positional behavior they exhibit. Their positional repertoire is not static through time, but rather changes with age. As primates age and body size increases, the manner in which animals navigate their environment responds to shifting biomechanical, nutritional, socio-behavioral and reproductive factors. In this study, I examined positional behavior in a colony of captive colobine monkeys, hypothesizing that locomotor and postural diversity will increase with age due to changing physiological and ecological processes. I predicted that as animals mature, their positional diversity will increase as they become more adept at negotiating their three-dimensional environments.

I examined age effects on positional behavior in silvered langurs (*Trachypithecus cristatus*) housed at the Columbus Zoo. Data were collected from January – August 2009 using instantaneous focal animal sampling on a breeding group containing four adults, two juveniles, and one infant. During each scan I recorded the focal animal's identity, maintenance activity, substrate, and postural (19 categories) or locomotor (12 categories) behavior. Chi-square tests were performed on the data set of 4504 scans.

Contrary to expectations, my analyses show that the number of observed positional behaviors did not change significantly with age, although the types of behaviors observed did change. Younger individuals displayed a greater range of behaviors while demonstrating elevated frequencies of climbing ($p = 0.0065$) and leaping ($p = 0.0004$). Use of hindlimb postures also showed an age effect, with propped-foot sitting becoming increasingly common in older individuals. Behaviors not associated directly with age may be explained by interacting factors, including age, sex, and reproductive state. I conclude that in this captive group of silvered langurs, diversity of positional behaviors and frequencies of specific locomotor activities covary with age, but that captive environments may be responsible for results at odds with those obtained from free-ranging populations.

INTRODUCTION & BACKGROUND

As an order, primates are a mobile taxon, and have a generalist body form that permits many different locomotor adaptations (Fleagle 1999). In contrast to many other organisms which are more sessile, primates spend much of their lives moving throughout the canopy or across the ground in search of food. The diversity of positional behaviors utilized by primates is unmatched in other mammalian groups, which makes them particularly fascinating subjects for the study of this behavior. Most primate locomotor behavior is related to foraging for food, rather than migration or finding mates as in many other vertebrates, and the dominant positional behaviors for a particular primate taxon vary based on habitat structure, ancestry, and, to a degree, diet (Fleagle 1982).

Additionally, primates are largely an arboreal radiation. The ability to navigate and maintain life activities in the trees required a new and, in many ways, unique set of anatomical and behavioral adaptations. Primates have evolved diverse adaptations to a variety of arboreal and terrestrial lifestyles, many of which focus on enabling new modes of posture and locomotion. Prehensile hands, feet, and tails, stereoscopic vision, the replacement of claws with nails, and other features found in primates have increased their ability to traverse the three-dimensional world of the trees in a way that most effectively meets the needs of each taxon.

Primate positional behavior consists primarily of two categories: posture and locomotion. Posture consists of stationary behaviors, such as sitting and standing, while locomotion encompasses the dynamic behaviors, such as walking, running, or leaping (Garber 2007). In general, postural behaviors are seen more often than locomotor behaviors (Rose 1974, McGraw 1998a). The study of positional activities is critical to understanding the lifestyle of primates, as these activities are the means by which primates navigate their environments to find food, avoid

predators, and interact with conspecifics. An understanding of positional behavior can also be valuable in understanding the evolutionary history of primate groups, as those animals better able to exploit their environments should have greater success in surviving and producing offspring (Napier 1967).

The selective pressures leading to the adaptations of the primate order are debated. The primary hypothesis in the early part of the 20th century claimed that the suite of primate features evolved to enable more effective arboreal living (Conroy 1990). One contrasting hypothesis is the visual predation hypothesis, arguing that the nailed hands and stereoscopic vision of early primates better enabled them to stalk and catch insects (Cartmill 1992). Another proposed idea, the angiosperm exploitation hypothesis, argues that primates evolved to feed on fruit, flowers, and nectar at the ends of branches (Sussman 1991). Whichever of these hypotheses is closest to the true adaptive origin of primates, all of these adaptations have enabled primates to find food, avoid predators, and move safely and gracefully throughout the arboreal environment (Cant 1992). Each primate taxon has additionally developed other morphological and behavioral adaptations which allow it to exploit its own adaptive zone, and these behavioral adaptations are studied as positional behavior.

Langurs and Positional Behavior

Colobines, the leaf-eating monkeys of the Old World, have achieved their greatest taxonomic diversity in Asia, and the most abundant and diverse of these are the langurs (Fleagle 1988). The taxonomy of langurs is hotly debated (e.g. Brandon-Jones 1984, Oates et. al. 1994, Collura and Stewart 1996, Osterholz et. al 2008), and there is currently no consensus regarding the number of species within the *Trachypithecus cristatus* group (Denise et. al. 2008). Colobines

are also suffering extensively from hunting, habitat destruction, and the pet trade; although they represent only 15% of primate species, nine of the 25 most endangered primates are colobines (Fashing 2006, Geissmann et. al. 2006). *T. cristatus* is currently listed as "Near Threatened" on the IUCN Red List, a designation downgraded from "Lower Risk" in 1996 due mainly to habitat destruction, hunting, and the pet trade (Nijman and Meijaard 2008).

The behavior of *Trachypithecus cristatus* has not been extensively studied in the past 15 years. While several general behavioral studies were conducted in the 1960s and 1970s (Furuya 1961, Wolf and Fleagle 1977), and a few studies in the early 1990s focused on diet and feeding behavior (Brotoisworo and Dirgayusa 1991, Kool 1993), most recent studies have focused on morphology (Shelmidine et. al. 2007, 2009) or genetics (Denise et. al. 2008, Roos et. al. 2008). However, the frequent reclassification, renaming, and reorganization of the langur species and genera make it difficult to discern which of these studies refer to currently-recognized species. *T. cristatus* has been known over the years as *Trachypithecus pruinosus*, *T. pullata*, *T. rutledgii*, and *T. ultima* (Nijman and Meijaard 2008).

A 1967 study of gray langur locomotion was one of the first to attempt an exhaustive study of the complete positional repertoire of a primate species (Ripley 1967). Eleven years later, Fleagle compared the locomotor patterns of two sympatric species of *Presbytis*, focusing also on feeding postures and habitat utilization (Fleagle 1978). Since then, however, positional behavior in langurs has not been extensively documented, especially relative to African colobines and cercopithecines; however, much can be learned from examining the behavior of their African relatives. Many positional studies have examined sympatric species of Old World monkeys, both colobines and cercopithecines, in Africa, generally finding that colobines favor sitting postures over standing postures, and that their low intermembral indices allow them to

excel at leaping more than do cercopithecines (Gebo and Chapman 1995, McGraw 1998a, Fleagle 1999).

Colobines often sit while consuming food, as their folivorous diet permits them to remain in one place for extended periods, taking advantage of the abundant food supply around them (McGraw 1998b). The importance of these sitting postures in the colobine positional repertoire is continually reinforced in study after study (Mittermeier and Fleagle 1976, Morbeck, 1977). However, most of these studies have lumped all forms of sitting into a single category, not distinguishing between behaviors with very different leg postures, which may have significant anatomical bases.

Ontogeny of Positional Behavior: This Study and its Context

Until recently, the ontogenetic aspects of positional behavior in primates have rarely been studied. Often, positional studies excluded juveniles, while noting that great variety existed between the positional patterns of adults and immature individuals (e.g. Fleagle 1978). Indeed, differences in body size alone should produce differences in positional repertoire; this has been demonstrated both between species (Fleagle and Mittermeier 1980, Crompton 1984, Fleagle 1985, Cant 1992) and within a single species (Doran 1993). Changes in the musculoskeletal system early in life also will have an effect on both locomotor and postural behaviors (Turnquist and Wells 1994). These changes reflect the young primate's growing motor skills as it moves away from its mother and begins traveling and foraging on its own, and also reflect the changing needs and maintenance priorities of adult animals. Studying the changes that occur with age will help primatologists understand the development of young primate dietary and locomotor independence, as well as the changing importance of different positional behaviors throughout

the life span. However, in general, the effects of ontogeny on positional behavior are little known and little studied (Doran 1997, Benzanson 2003).

While some researchers have recently focused on the age at which a juvenile's positional repertoire becomes adult-like (Lawler 2006, Benzanson 2009), this research has not accounted

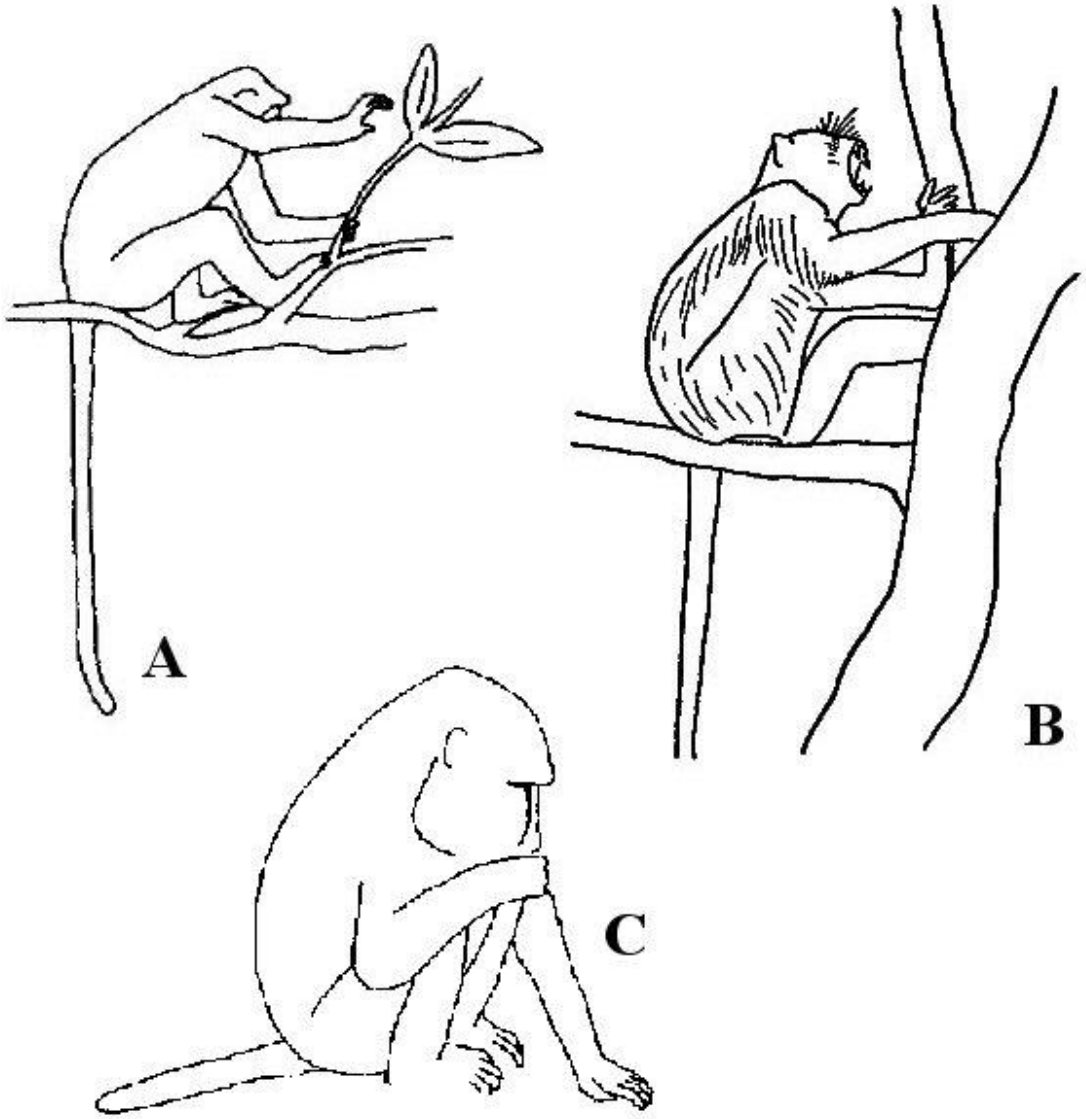

Fig. 1. Variants of the basic postural mode "sit." A: Extended-leg sit, with the hips and knees extended (Hunt et. al. 1996). B: Foot-prop, with the hips flexed and the feet planted against a vertical support (Ripley 1977). C: Tucked-leg sit, with both the hips and knees flexed (Hunt et. al. 1996).

for further changes that may occur as an adult individual continues to age. Others have focused solely on locomotor behavior and have not accounted for postural modes (Crompton 1983, Doran 1997). Three fairly recent papers, however, have examined the ontogeny of positional behavior in four species of Asian colobines and two species of macaques (Dunbar and Badam 1998, Wells and Turnquist 2001, Workman and Covert 2005). These concluded that older infants and juveniles had a wider diversity of positional behavior than adults and also exhibited a greater proportion of locomotor activity throughout the day, but found there was little variation in the number of behaviors exhibited within the two age categories of "adults" and "immatures."

In this study, I examined differences between adults and juveniles as separate age categories, as well as differences along the spectrum of age. Recognizing the importance of sitting postures in the colobine positional repertoire, I also differentiated between multiple forms of sitting, to see whether this also varied with age. I tested three hypotheses:

1) The proportion of locomotor behavior in the total repertoire will be higher for younger individuals. Younger individuals will likely spend more time in active play behavior, and will also need to explore their environment and learn how to navigate through it.
2) The frequency of different types of sitting behavior will change with age. Morphological changes associated first with ontogeny and then with senescence may have an impact on the variation within this broad posture category.
3) Locomotor and postural diversity will increase with age, as the social and ecological needs of the primates become more demanding. As these needs change with age and young primates become more confident and skilled in their ability to move through their environment, the number of behaviors that they are able to perform will increase.

MATERIALS & METHODS

Study Group

All data were collected from a captive breeding troop of six silvered langurs housed at the Columbus Zoo and Aquarium in Columbus, Ohio, from 26 January to 6 August 2009. The group was composed of one adult male (Digby, age 4 at the beginning of the study), three unrelated adult females (Patti, Gumby, and Eggnog, aged 9, 7, and 4, respectively), and two juvenile males (Pokey and Ollie, aged 18 months and 5 months). A third male juvenile (Fernando) was born to Patti on 6 July, and data were thereafter collected on his early positional development for the first month of life (Table 1). Digby is the sire of all three juveniles, and Gumby is the mother of Pokey and Ollie.

The langurs could be individually identified by facial features, tail characteristics, and, in the case of the juveniles, body size and/or coat color. I had learned to identify all individuals in the breeding group during a previous study. Feeding occurred daily at approximately 09:00 and 15:30 hours.

Study Site

The langur exhibit consists of two indoor enclosures and one outdoor enclosure, each linked to the others by small doors. These enclosures were shared with a bachelor troop, but on no occasion were both groups allowed access to the same area. Beginning in May, the two troops were allowed free access between their indoor and outdoor exhibits on alternating days; this access was restricted in the week following the birth of Patti's infant in July so that keepers and docents could more easily track the infant's progress. When given free access between the indoor and outdoor enclosures, the group tended to move as a unit between them; thus, keeping

Fig. 2. One of the indoor exhibits. The scaffold system and synthetic vine network are clearly visible in the foreground, while one of the pillars is visible in the background to the right. Pictured is adult male Digby.

track of all members of the group rarely posed a challenge. All parts of the exhibit made available to the langurs during the day were visible from at least some parts of the guest viewing area.

The indoor enclosures each contained a metal scaffold system approximately 5 meters tall, as well as two stone pillars approximately 0.3 meters in diameter and 2 meters tall. Each also contained a ladder, several food bins, and synthetic vines leading from one landmark to another. These enclosures made particular use of vertical space, with stone staircases allowing keepers to have access to all areas of the exhibit. The floor of the exhibit was also stone. A

glass wall separated the enclosures from the guest viewing area where I made my observations (Fig. 2).

The outdoor enclosure contained a protruding brick doorway, two large synthetic trees, several small trees, and three stone ledges. The area was closed off by netting held up by wire cables, each of which was on occasion used as support by the langurs. Food was provided on platforms resembling shelf fungi on the sides of the large trees, and also occasionally through the netting. This enclosure also contained a network of vines between the major landmarks.

Data Collection

Data collection occurred preferentially during the summer, between the hours of 9:00 and 19:00. During the winter and spring, data were collected in 3-4 hour blocks; during the summer, it was collected in 6-8 hour blocks. All data were collected using instantaneous focal animal sampling at two-minute intervals, cycling through the group such that at least a 12-minute period separated any two observations for a given individual (Altmann, 1974). One hundred and fifty hours and eight minutes of data were collected, for a total of 4,504 observations. This method allows ample time between observations to prevent sampling bias, and the high number of observations allow it to approximate continuous sampling (Doran 1992).

At each interval, data were taken on 6-8 variables. For all individuals, time, identity, maintenance activity, positional behavior, and substrate were recorded, as well as whether the individual was in the indoor or outdoor enclosure. For individuals under 18 months of age, I also noted if the individual was moving or resting independently, or if it was in close proximity to (i.e., touching) an adult. After Patti's infant was born, alloparenting data were also recorded at

each interval, noting which group member was holding the infant, or if the infant was moving independently.

Seven maintenance categories were recognized:

1) Allogroom – grooming of another group member
2) Feed – behavioral activity associated with selecting, handling, or ingesting food.
3) Nurse – an infant or juvenile is nursing from its mother
4) Rest – any observation in which the animal is inactive
5) Self-groom – includes scratching and self-examination
6) Social – non-grooming social activity, such as play or aggression
7) Travel – the individual is moving from one part of the enclosure to another

A sample data sheet is provided in Table 2. In addition, a list of recognized positional behaviors and their definitions is provided in Table 3; these behaviors are based on those reviewed by Hunt and colleagues (Hunt et. al. 1996). Specifically, four forms of sitting were recognized, based on two criteria: (1) whether the hips and knees were flexed or extended, and (2) whether both hindlimbs exhibited the same posture. The result was four forms referred to as:

1) Tucked-leg sit, with both the knees and hips flexed
2) Extended-leg sit , with both the knees and hips extended
3) Two-foot prop, with the knees extended and the hips flexed.
4) One-foot prop, with the knee extended and the hip flexed in one leg, and either a tucked or extended posture in the other leg

Other combinations of these criteria were not observed. These forms, as well as all other positional behaviors observed more than 10 times, are defined in Table 3. Substrates recognized varied between the indoor and outdoor enclosures, but are detailed in Table 4. The chi-square

statistic was used to test for differences between individuals in the frequency of various positional modes, proportion of locomotor behavior, and the number of behaviors exhibited. The infant born during the study was excluded from analysis in this paper, as the study ended when he was only 1 month of age and had only just begun to move on his own.

RESULTS

A general table of positional repertoire is included, showing the percent distributions of behaviors for each individual and the average values for the group (Table 5). By far the most

Fig. 3. Two langurs exhibiting the basic tucked-leg sitting position, by far the most common positional behavior observed.

common positional behavior in all subjects was the basic tucked-leg sit (Fig. 1C, Fig. 3). This accounted for between 52-74% of all data points for all individuals, with an average group value of 66%. Comparisons of data indicate that tucked-leg sitting decreases with age (χ^2=34.954, $p < 0.0001$, Fig. 4).

Other forms of sitting also showed an age relationship. Extended-leg sitting was most common in older juveniles and younger adults, with a (χ^2=81.802, $p<0.0001$, Fig. 5). A two-foot propped posture, with both hips flexed and the knees extended, and both feet planted against a vertical support near the level of the head, was more common in all adult individuals than in juveniles (χ^2=68.098, $p < 0.0001$, Fig. 6). This significance value remains when combining two-foot prop and one-foot prop sitting styles (Fig. 7).

Climbing and leaping frequencies were greater in younger individuals. The higher frequencies of climbing and leaping in immature individuals were significant at levels of p=0.0065 and p=0.0004, respectively (Fig. 8).

Younger individuals were generally more active than older individuals, although all members of the group were largely sedentary in their behavior. Postural behavior dominated the data set, with locomotor behavior comprising only 1.58-8.45% of all scans. However, there is a clear decline throughout the entire spectrum of age, with the young juvenile being more active than the older juvenile, in turn more active than the youngest adult, etc. This difference was also significant, at a level of $p < 0.0001$ (Fig. 9).

Finally, the number of behaviors exhibited throughout the study ranged from 12 in the second-oldest group member to 23 in the young juvenile. A pattern seemed to exist with a greater locomotor diversity in juveniles; however, the age differences in number of modes displayed was not significant (p=0.3947) (Fig. 10).

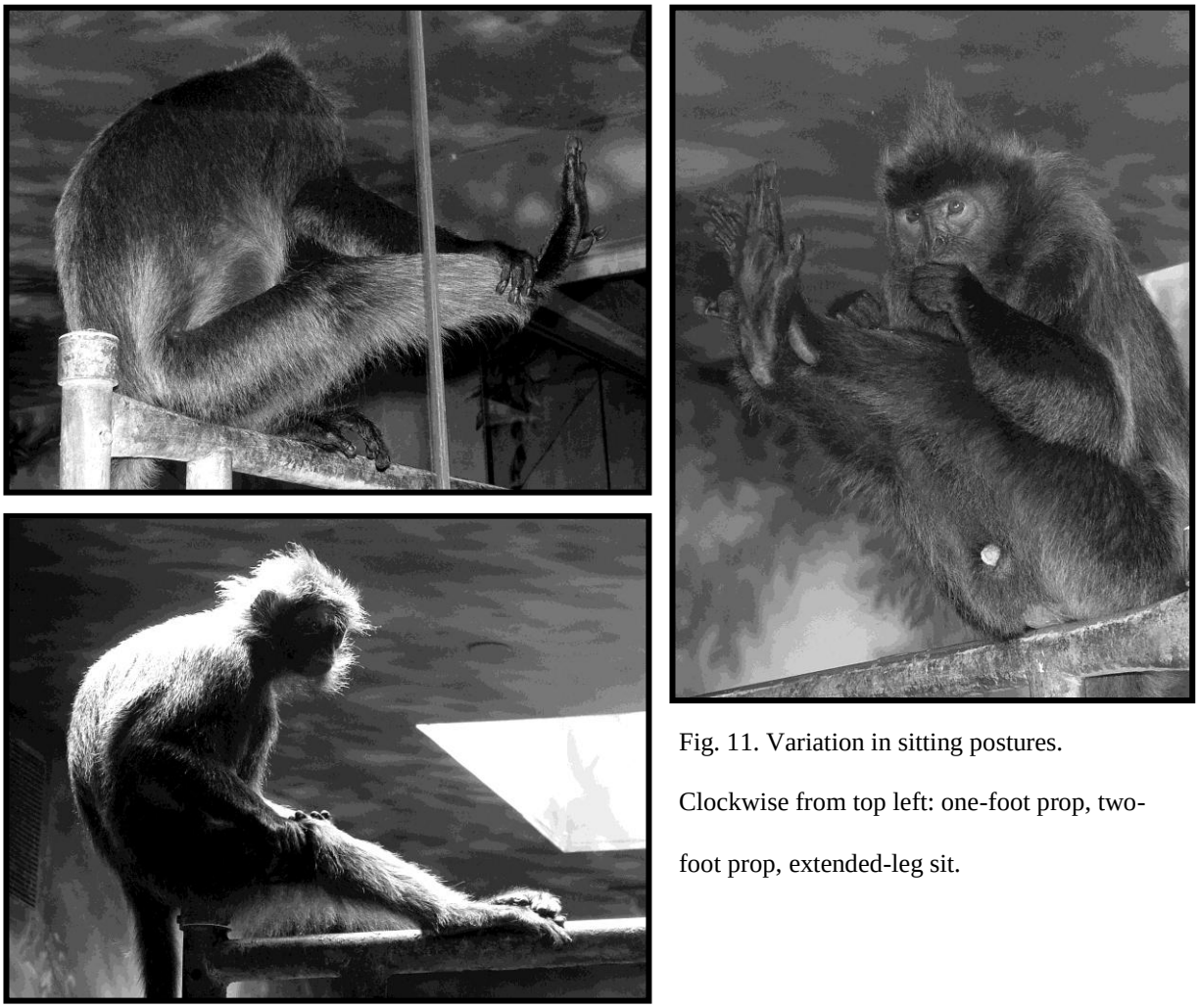

Fig. 11. Variation in sitting postures. Clockwise from top left: one-foot prop, two-foot prop, extended-leg sit.

DISCUSSION

Due to their high-fiber, low-energy diet and need for extended periods of digestion, langurs, like most colobines, are energy-minimizers, and are quite sedentary relative to frugivorous Old World monkeys (Brotoisworo and Dirgayusa 1991, Kool 1993). The spatial and temporal distribution of fruit and insects, as well as the mobility of insects, forces frugivorous and insectivorous primates to remain standing and continually move between food patches to meet their daily energy requirements. However, folivores such as langurs are able to remain seated and take advantage of the abundance of food around them, which is readily available at all

times and is not mobile (McGraw 1998b). As langurs age, they become even more sedentary, with frequency of locomotor behavior decreasing fairly steadily from 8.45% in a young juvenile male down to a mere 1.58% of all sampling intervals in the oldest individual, a 9-year-old female. This may reflect a decrease in active play behavior. Social play occurred almost exclusively between the two juveniles, while the adults rarely engaged in play behavior with either each other or the juveniles (Figure 12).

It is also possible that adults move less because as higher-ranking members of the group, they are able to commandeer prime feeding locations, leaving younger individuals to constantly move back and forth between the food source and an appropriate place to consume their food. Another explanation for the increasingly sedentary behavior of adults is that adults do not wish to unnecessarily risk falling. High in the trees, or on the scaffold, as the case may be, falling is a serious hazard, and perhaps adults have learned that remaining stationary increases their stability.

Other possible causes for the decline in relative frequency of locomotor behavior with increasing age include the negative effects of aging on the bones or joints, or a lower metabolic rate in older individuals. A more in-depth anatomical and physiological study of langurs of varying age classes would need to be conducted in order to determine the likelihood of these suggestions. The greatly elevated frequencies of climbing and leaping behaviors in young individuals could also largely be explained by the much higher frequency of locomotor behavior in general.

The significant variation in sitting postures associated with age provides an interesting perspective on the long-recognized fact that "sitting" is one of the most important positional behaviors in a colobine's repertoire. For a taxonomic group in which some type of "sit" comprises such a large portion of its positional inventory, it is important to distinguish between

those types to get a true picture of the animal's behavior and the way in which different age or sex classes interact with their environment (Fig. 11). "Sit" is simply not descriptive enough to encompass the considerable variation of behavior that is unceremoniously dumped into one category.

The diversity in sitting postures is largely expressed in the positions of two joints: the hip and the knee. Virtually every combination of flexing or extending those two joints was observed, save for flexing the knee and extending the hip, which would result in a kneeling-type posture. Even outward rotation of the flexed hips and knees was observed, with three scans showing a "butterfly sitting" posture from the youngest adult female. While a position with flexed hips and knees (the tucked-leg sit) was the most common posture found in all group members, it was slightly less popular with juveniles, who often favored a fully extended pose when stationary.

Although a trend at first seemed to exist associating increasing age with decreasing positional diversity, this pattern was not significant, nor did it approach significance. This may contradict previous studies which showed a greatly elevated variety of behaviors in juveniles of two macaque species and four langur species (Dunbar and Badam 1998, Wells and Turnquist 2001, Workman and Covert 2005). Here, the null hypothesis was not rejected, and while the trend of the data seems in the opposite direction of my original hypothesis, without statistical significance it is impossible to say whether more data would give a clearer answer.

These different findings may be a result of different study conditions. It is important to note that of the other studies demonstrating this positional diversity in immature individuals, one was conducted at a rescue center (Workman and Covert 2005), one at a provisioned free-ranging site (Wells and Turnquist 2001), and one with a mixture of laboratory, free-ranging, and

provisioned free-ranging animals (Dunbar and Badam 1998). While it is often necessary to work with what is available, especially with studies of ontogeny in which captive settings allow a more complete knowledge of the age and history of the study group members, a study of non-provisioned free-ranging animals would give the best approximation of natural behavior. It is possible that in these captive or provisioned conditions, juveniles have more time for play, during which they are able to cultivate a much more diverse positional repertoire.

Implications and Future Work

Most studies of primate behavior which attempt examine the impact of selective forces are best conducted in the wild, where these forces are still in action, rather than in the controlled environment of a zoo. The influences of foraging needs, predator avoidance, and intergroup conflict, if existing at all in captivity, do not affect behavior to the same degree as in the wild. Zoo populations are by their very nature a small sample size, and captivity may well have an effect on behavior also. Captive studies study may lend direction and support to future research, but the results cannot be thoroughly demonstrated to be accurate in the wild without a corresponding field study.

However, zoo studies also have their advantages. By studying a captive-born population, I had access to the animals' dates of birth and detailed information about their history. In addition, I had a clear and close view of the monkeys, which allowed me to easily and clearly distinguish the subtle differences between sitting postures that may have seemed very similar from a distance; this would have been much more difficult in the wild. Additional data collected under natural conditions, and with a larger sample size would reinforce my conclusions that silvered langurs do not follow the trend observed in previous studies of greater positional variety

in immature individuals. A field study would also help to confirm whether the patterns of sitting style found in this group are similar to those found in wild populations, or if they are instead heavily influenced by their captive environment and the nature of their zoo enclosure.

In addition, future study should address the anatomical changes that occur with age to determine whether these might have an impact on positional behavior and diversity. For example, the foot-prop posture common in older individuals is anatomically similar to the extended-leg sit found more in younger animals, simply involving a flexed hip rather than an extended one. Could changes in the hip joint in old age have an effect on the way langurs sit, such that flexing the hip is more stable or comfortable than extending it? A closer examination of langur morphology may help answer these questions.

SUMMARY & CONCLUSIONS

1) The Columbus Zoo langurs spent approximately 87% of their time in various sitting postures, 2% sprawled, 2% standing either quadrupedally or bipedally, and 1.5% walking. Leaping, climbing, and running each accounted for less than 1% of all scans.

2) Younger langurs displayed elevated frequencies of climbing and leaping, and spent a higher proportion of their time in locomotor rather than postural modes of positional behavior. They displayed lower frequencies of sitting postures in general due to this greater time spent in locomotion.

3) Older langurs displayed elevated frequencies of tucked-leg sitting and foot-prop postures.

4) The extended-leg sitting posture was common in older juveniles and young adults, perhaps displaying a transition phase.

5) Contrary to predictions and to past studies in this area, no significant difference was found in the number of positional behaviors observed in individuals of different ages. This suggests that the higher positional diversity of older juveniles noted in other studies may not be universal. In some groups, the positional repertoire of adults and immatures may change to include different behaviors or different frequencies of behaviors while remaining just as diverse.

6) Combining multiple distinct postures (i.e. the various forms of sitting) into a single category can obscure the diversity that exists within the category. Had all of the sitting postures (tucked-leg, extended-leg, and foot prop) been grouped together, it is likely that the age differences would have gone largely unnoticed. Thus, it is important to distinguish between similar but distinct behaviors, especially when these behaviors comprise a portion of the overall positional repertoire as large as "sitting" does for colobine monkeys.

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FIGURES AND TABLES

Name	Sex	Age (mo.)	Date of Birth	Relationships
Patti	F	109	12/1/1999	Mother of Fernando
Gumby	F	93	4/16/2001	Mother of Pokey, Ollie
Digby	M	58	3/13/2004	Sire of Pokey, Ollie, Fernando
Eggnog	F	48	1/10/2005	unrelated
Pokey	M	18	7/7/2007	Offspring of Digby, Gumby
Ollie	M	5	8/8/2008	Offspring of Digby, Gumby
Fernando	M	-6	7/6/2009	Offspring of Digby, Patti

Table 1. The Columbus Zoo breeding troop of silvered langurs. Names, ages in months at the beginning of the study, date of birth, and relationships to other group members are listed. The infant Fernando born during the study was excluded from analysis.

Date	Time	Individual	Age (Mo)	Sex	Location	Activity	Positional Behavior	Substrate	Ind.?	Hold baby
7/6/2009	13:58	Patti	115	F	Indoor	R	S	R	-----	E
7/6/2009	14:00	Gumby	97	F	Indoor	R	S	R	-----	P
7/6/2009	14:02	Digby	63	M	Indoor	R	So	P	-----	P
7/6/2009	14:04	Eggnog	53	F	Indoor	R	S	P	-----	P
7/6/2009	14:06	Pokey	23	M	Indoor	R	S	P	-----	P
7/6/2009	14:08	Ollie	10	M	Indoor	R	S	V	N	P
7/6/2009	14:10	Fernando	0	M	Indoor	R	G	P	N	E

Table 2. Sample data sheet.

Behavior	Description
Bipedal stand	Supporting its weight plantigrade on the hind feet, with its spine upright and perpendicular to the horizontal support. May be using one or more hands for balance, but does not support weight on them.
Cling	Holding on to a vertical support, pulling its body close to the support and keeping its spine parallel to it.
Extended-leg sit, or, sit-out	Sitting with the hindlimbs stretched out, with the ischia bearing most of the body weight.
Two-foot prop (or "foot prop")	Sitting with the hips flexed and knees extended, such that the feet are resting against a vertical substrate.
Grasp	Supported by grasping the dorsal or ventral fur of an adult.
Hang	Below the support, clinging to the support with its hands or feet.
One-foot prop	Sitting with one leg fully extended upwards and resting against a vertical substrate. The other leg is either extended or tucked.
Sprawl	Resting with its ventral side directly on the horizontal support.
Stand	Supporting its weight plantigrade on all hands and feet, keeping its spine parallel to a horizontal support.
Tucked-leg sit, or, sit-in	Resting with its weight supported by the ischia and feet, with the hip and knee tightly flexed, bringing the feet close to the ischia.
Climb	Ascending or descending along a vertical support.
Leap	Propelling itself through the air from one support to another, primarily using its hindlimbs.
Roll	In play, tumbling head over feet or from side to side
Run	Moving pronograde along a horizontal support at a rapid pace.
Walk	Moving pronograde along a horizontal support at a slow to moderate pace.

Table 3. Major categories of positional behavior as defined in this study. This table includes all behaviors which occurred more than 10 times. The total number of behaviors observed is much greater: 19 postural behaviors and 12 locomotor behaviors.

Substrate	Location	Description
Bin	Indoor	Small rectangular bins in which food was provided; attached to scaffold or walls
Cable	Indoor/Outdoor	Wire cables holding up the exhibit netting or operating the doors between exhibits
Crossbeams	Indoor	The flat diagonal crossbeams of the scaffold system
Door	Outdoor	A protruding brick door which extends from the wall in between the entrances to the two indoor exhibits
Doorway	Indoor/Outdoor	The small, square doorways leading between the indoor and outdoor exhibits
Fungus	Outdoor	The flat shelf fungus-shaped platforms on which food was provided in the outdoor exhibit
Ground	Indoor/Outdoor	The stone (inside) or grassy (outside) floor of the exhibit
Ladder	Indoor	The bamboo ladders leaned against the indoor exhibit walls
Large branch	Outdoor	Large, horizontal branches of the large synthetic trees
Netting	Outdoor	The rope netting used to enclose the outdoor exhibit
Pillar	Indoor	One of the two stone pillars (approx. 1 foot in diameter and 5 feet tall) found in each indoor exhibit
Rail	Indoor	A cylindrical rail around the edges of the high platforms in the indoor exhibits
Scaffold	Indoor	A tall scaffold system in each indoor exhibit, with horizontal and vertical cylindrical beams
Small branch	Outdoor	Branches on the small trees in the outdoor exhibit, small enough to be grasped in the langurs' hands
Vine	Indoor/Outdoor	Synthetic vines approximately 2-3" in diameter which spanned between major landmarks of the exhibits
Wall	Outdoor	Small ledges and nooks in the brick wall between the indoor and outdoor exhibits

Table 4. List of recognized substrates in the indoor and outdoor langur exhibits. Substrate for leaping was noted as X->Y, such that X was the substrate the subject took off from, and Y was the substrate on which the subject landed.

Individual	Tucked-leg Sit	Extended-leg Sit	Two-foot Prop	Grasp	Sprawl	Walk	Stand	One-foot Prop
Patti	74.14	13.07	6.75	0.00	1.15	0.72	0.86	2.01
Gumby	73.85	15.09	6.32	0.00	0.43	1.15	0.86	0.72
Digby	69.06	13.53	7.05	0.00	6.19	1.29	0.58	0.29
Eggnog	62.50	22.56	5.89	0.00	0.86	1.44	1.15	1.87
Pokey	63.60	18.71	4.17	0.00	1.87	2.01	1.29	1.01
Ollie	52.81	5.18	1.44	24.46	1.15	2.45	2.59	0.14
Grand Total	**66.00**	**14.69**	**5.27**	**4.07**	**1.94**	**1.51**	**1.22**	**1.01**

Individual	Leap	Climb	Bipedal Stand	Run	Other
Patti	0.14	0.72	0.14	0.00	0.29
Gumby	1.01	0.14	0.29	0.00	0.14
Digby	0.43	0.00	0.14	0.43	1.01
Eggnog	0.29	1.01	0.29	0.29	1.87
Pokey	2.16	1.01	1.15	1.15	1.87
Ollie	1.29	1.73	1.58	1.73	3.45
Grand Total	**0.89%**	**0.77%**	**0.60**	**0.60**	**1.44**

Table 5. Positional behavior repertoire for the Columbus Zoo silvered langur troop. Numbers given are percentages of all scans. "Other" encompasses all behaviors which did not comprise more than one half of one percent of the scans for the whole group.

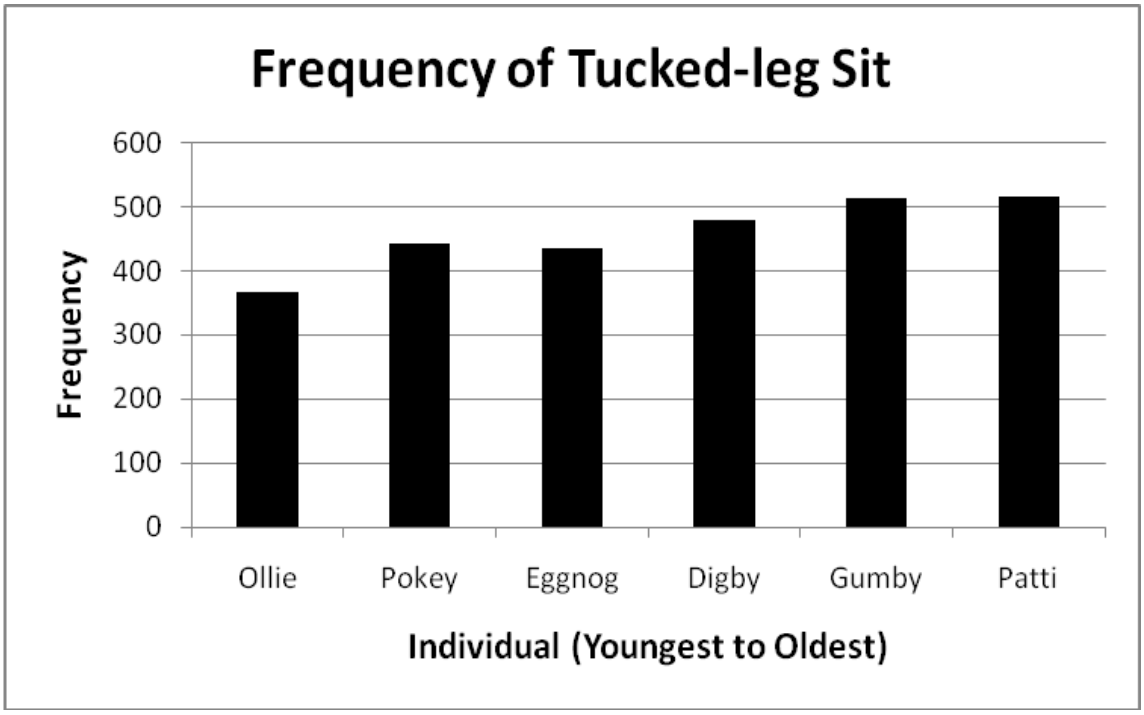

Fig. 4. Frequency of tucked-leg sitting posture by age. This increase in tucked-leg sitting with age is largely a function of increased sedentary behavior, and is significant at a level of $p < 0.0001$.

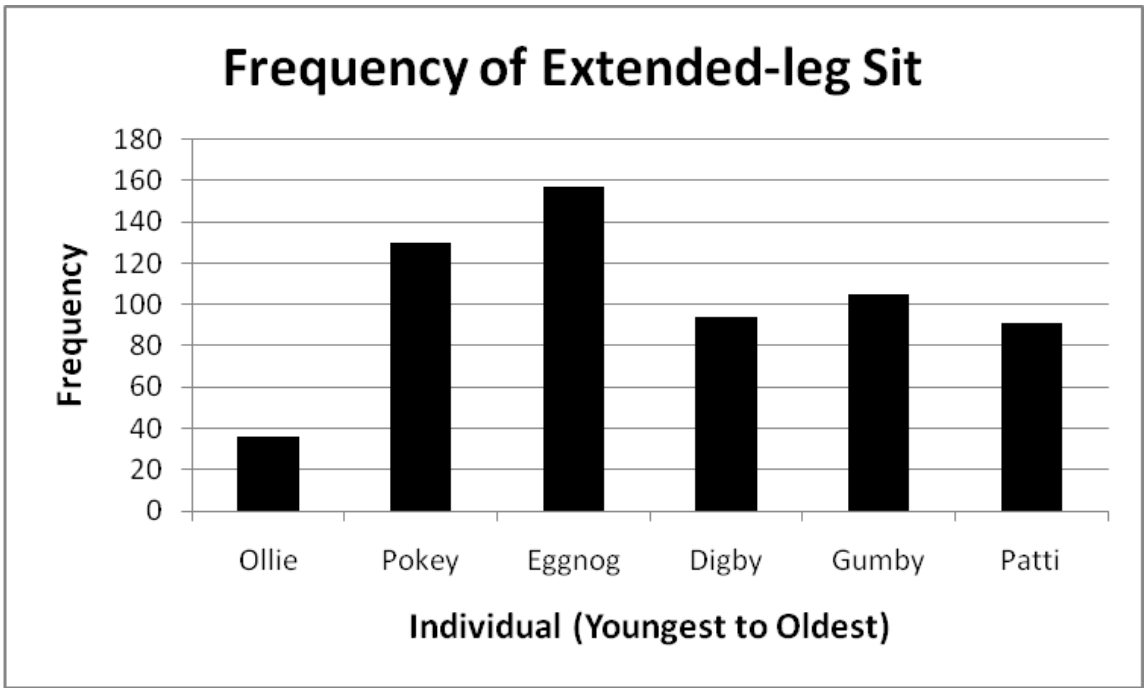

Fig. 5. Frequency of extended-leg sitting posture by age. This increase in tucked-leg sitting in older juveniles (Pokey) and younger adults (Eggnog) is significant at a level of $p < 0.0001$.

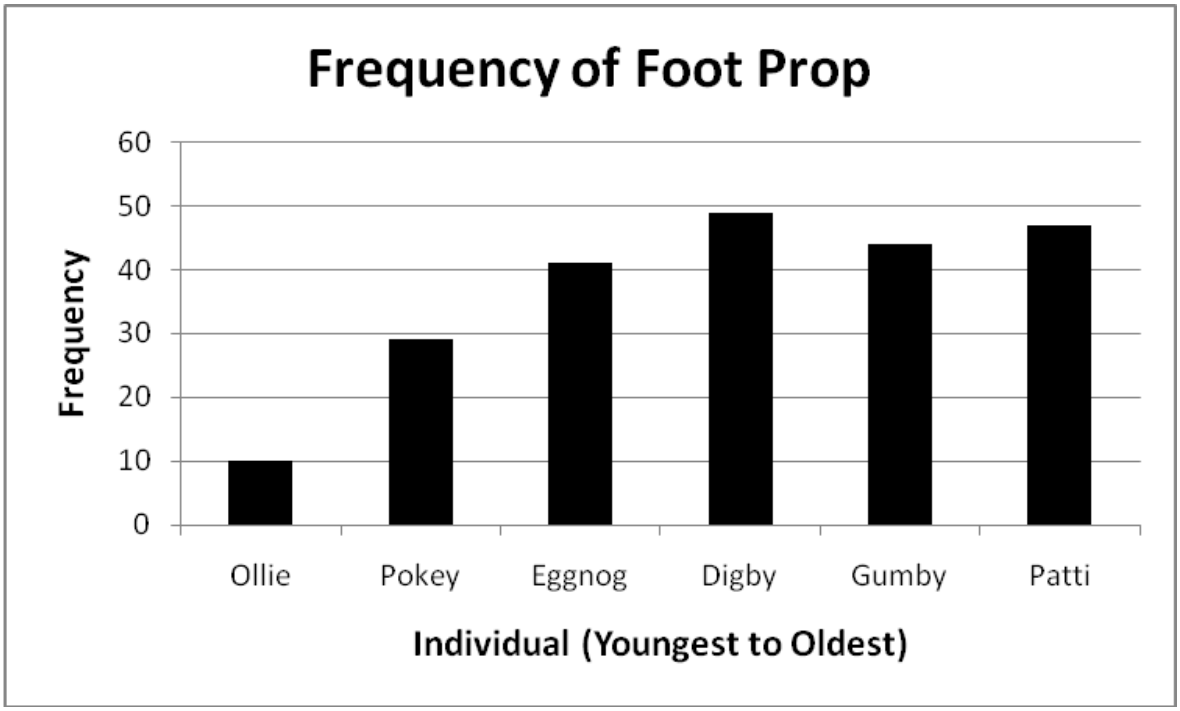

Fig 6. Frequency of two-foot prop sitting posture by age. This increase in propped-foot sitting in adults is significant at a level of $p < 0.0001$.

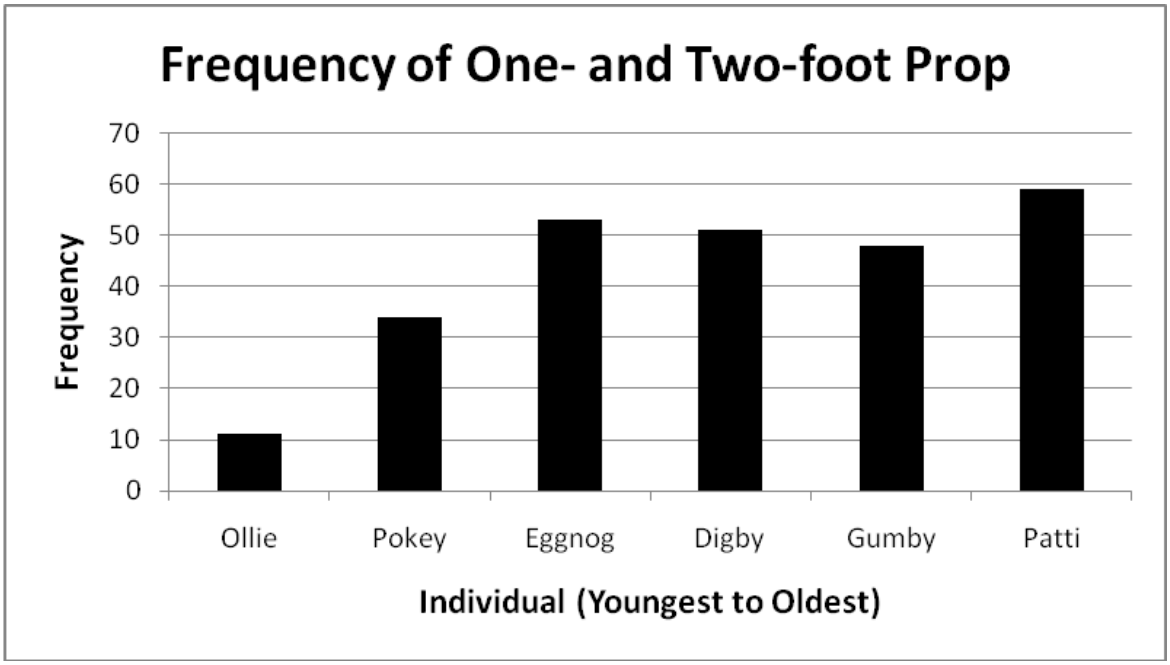

Fig. 7. Frequency of one-foot and two-foot prop postures combined. This increase in propped-foot sitting in adults is also significant at a level of $p < 0.0001$.

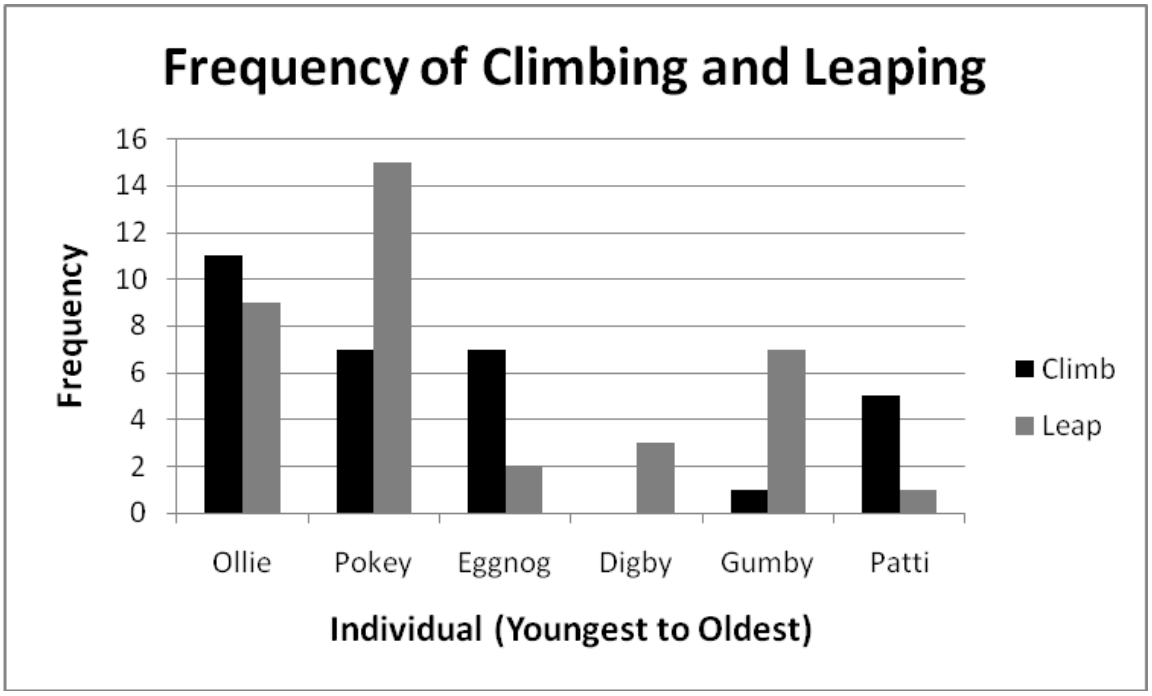

Fig. 8. Frequency of climbing and leaping. Climbing behavior was more common in young and old individuals, and less common in mid-aged individuals ($p = 0.0065$). Leaping was most common in juveniles ($p = 0.0004$).

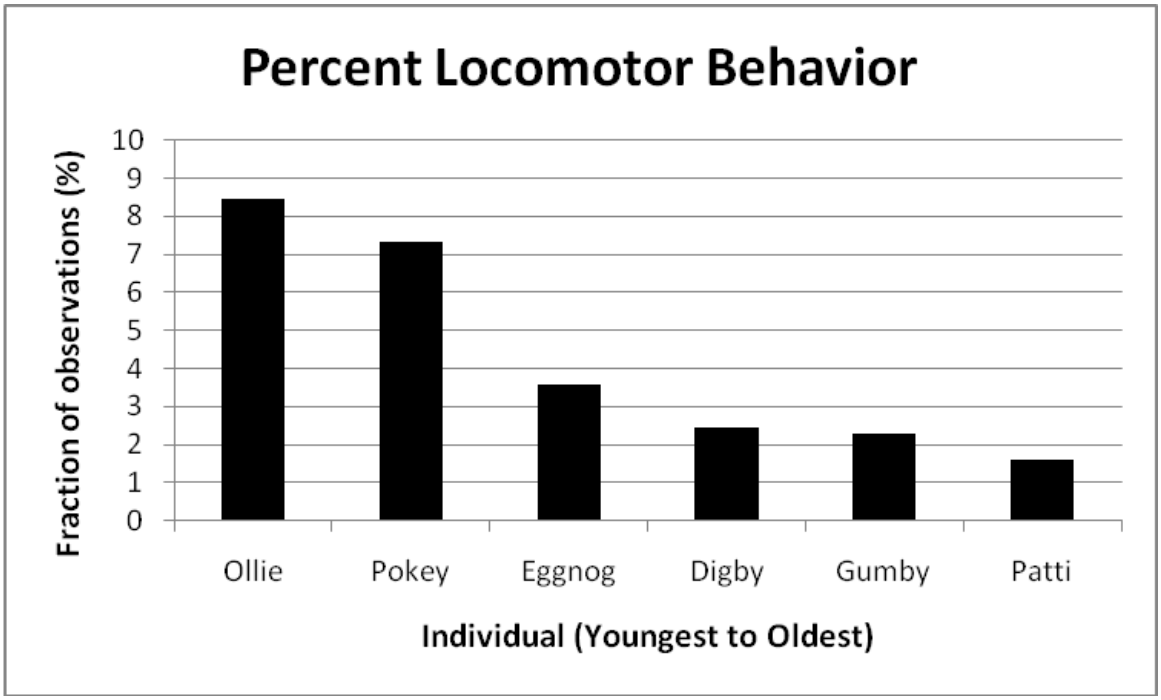

Fig. 9. Frequency of locomotor behavior as a percentage of total behavioral repertoire. This decrease in locomotor behavior with age is significant at a level of $p < 0.0001$.

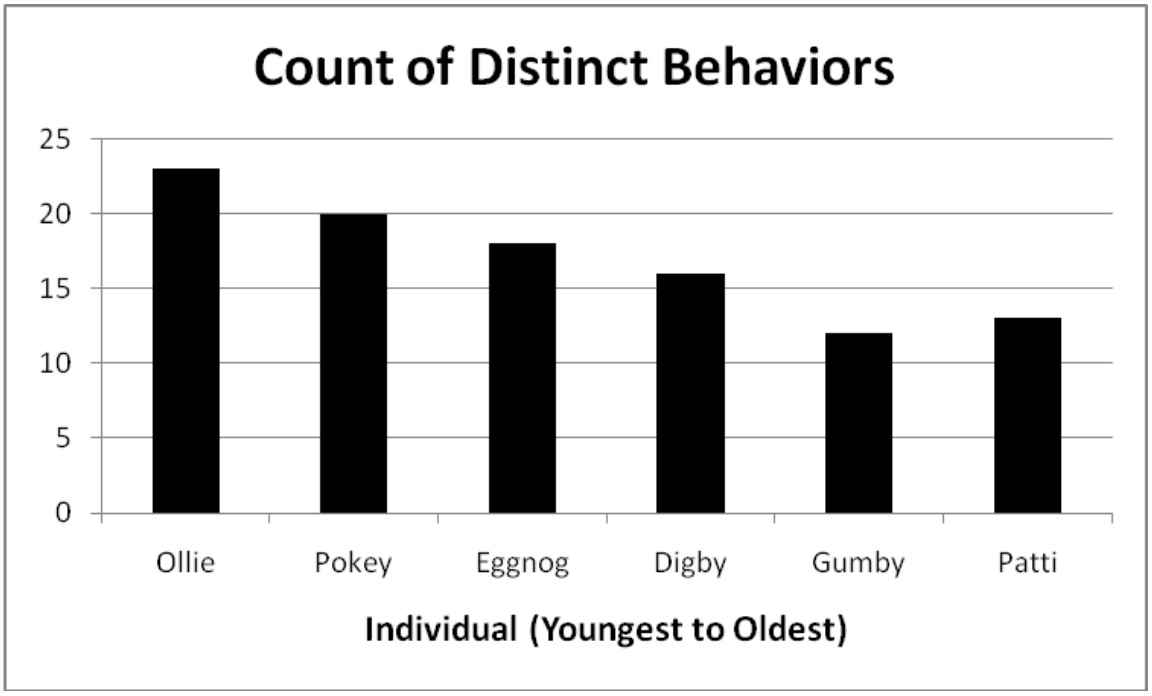

Fig. 10. Count of distinct positional behaviors observed throughout the study. This observed decrease in positional diversity was not significant ($p=0.3947$).

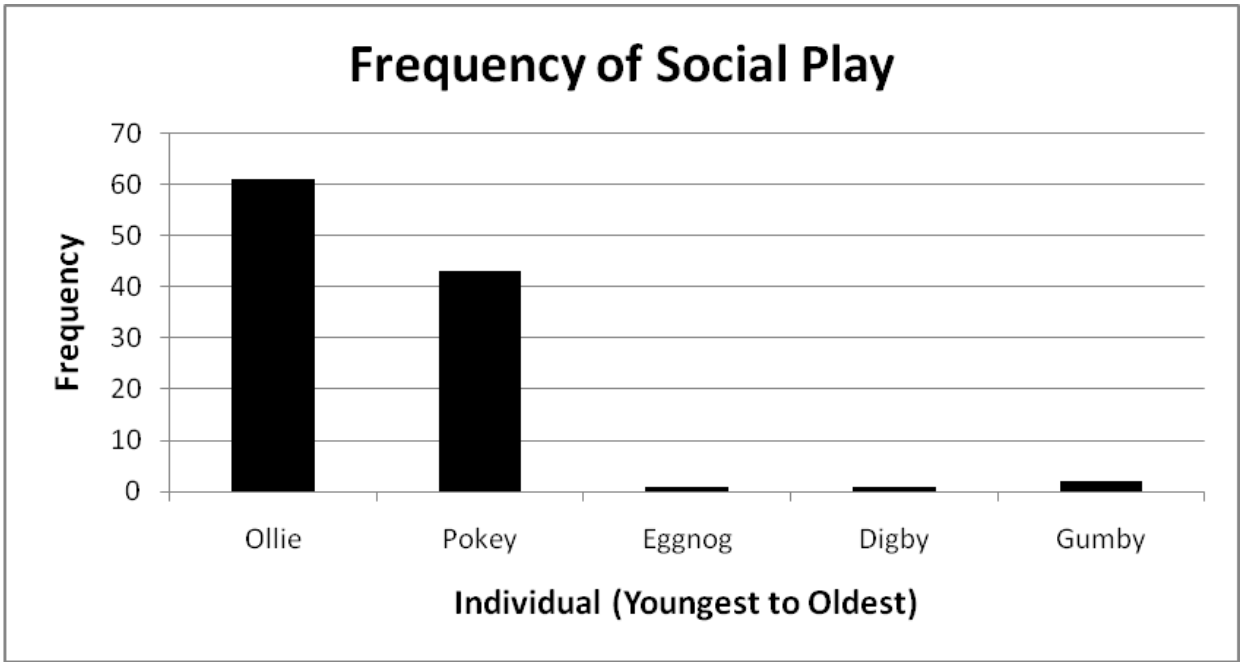

Fig. 12. Social play was found almost exclusively in the juveniles, and was not observed at all in the oldest female (Patti). This difference is significant to a level of $p < 0.0001$.